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Mendocinia, a Subholostean Fish from the Triassic of Argentina

By Bobb Schaeffer

Although extensive marine and continental Triassic deposits occur in various parts of South America (Weeks, 1947; Kummel and Fuchs, 1953), the fresh-water Cacheuta series and its equivalents in northern Argentina are among the few Triassic deposits on that continent which have thus far yielded fossil fishes in some abundance and diversity. Intensive studies on Triassic fishes from other parts of the world during the last three decades have demonstrated the importance of this part of the Mesozoic in relation to the palaeoniscoid-holostean transition. The Triassic fishes of South America, particularly from Argentina and Brazil, should provide interesting additional evidence on this phase of actinopterygian evolution.

The fishes from the Cacheuta and equivalent beds have been described briefly by Rusconi (1946a, 1946b, 1946c, 1947, 1948, 1949), Cabrera (1944b), and Bordas (1944). Unfortunately, these descriptions do not give adequate consideration to the diagnostic characters and hence do not allow accurate taxonomic allocation.

The present study is based on a collection of fishes from the Cacheuta series recently presented to the American Museum of Natural History. Most of the specimens may be referred to the genus *Mendocinia* Bordas, and the following remarks are confined to that form.

The drawings were prepared by Michael Insinna, who also assisted in checking many of the observations and measurements. The photographs were taken by Elwood Logan.

GEOLOGIC OCCURRENCE

The Cacheuta series is part of the extensive continental Triassic sequence occupying the San Juan-Mendoza basin in northern Argentina. Following extrusive igneous activity during the late Permian and perhaps the first part of the Triassic, and a subsequent interval during which the lavas were eroded, the Triassic sediments were deposited in this basin to a depth of about 2500 meters.

Recent studies of the best exposures in the provinces of Mendoza, San Juan, and La Rioja have been summarized by Groeber (1952). The term "Cacheuta series" is apparently usually restricted to the beds exposed between the towns of Potrerillos and Cacheuta in the Province of Mendoza, although Chiotti (MS) also uses the term for the essentially identical stratigraphic sequence between the towns of Challao and San Isidro, which are just west of the city of Mendoza.

In the vicinity of Challao, where the *Mendocinia* locality is located, the Triassic section has been studied in detail by Chiotti. The basal member, called the Conglomerado Colorado, lies disconformably on a series of porphyries of presumed Permian age. It is about 400 meters thick. Above this are the Estratos del Cerro de las Cabras, consisting of 700 meters of mostly sandstone and shale with plant remains. The succeeding unit, called the Estratos de Potrerillos, is represented by 550 meters of alternating sandstones, fine conglomerates, shales, and tuffs. It contains an abundant flora described by Frenguelli, also *Estheria, Semionotus* sp. (cited by Groeber, 1952, p. 49), and *Mendocinia*. The overlying Estratos de Cacheuta, about 40 meters thick in this area, are made up of bituminous shales with some plant remains and *Estheria*. The upper 250 meters represent the Estratos de Victor which are composed of alternating sandstones, shales, and tuffs. The Victor beds are regarded by some (Groeber, 1952, p. 50) as a facies of the Estratos de Cacheuta.

The section between Potrerillos and Cacheuta has a similar subdivision, except that the top unit, named the Estratos de Rio Blanco, is stratigraphically higher than the Victor. From this area Cabrera (1944a, 1944b) has described a fish, *Gyrolepidoides creyanus,* which he considers to be close to the Karroo *"Oxygnathus"* (see Brough, 1931, p. 238), and a brachyopid amphibian, *Pelorocephalus mendozensis*. Both occur in the Estratos del Cerro de las Cabras.

The fishes described by Rusconi were obtained from various localities in the vicinity of Challao, Cacheuta, and Los Paramillos de Uspallata (see Rusconi, 1954, pp. 130–134).

The age of the Cacheuta series and its equivalents has been the subject

of much recent deliberation. Although long regarded as Rhaetic (Geinitz, 1876), the character of the indigenous flora has suggested to some investigators (see Groeber, 1952, p. 46) that a major portion of the Triassic is represented. Chiotti (MS), for instance, is of the opinion, apparently on the basis of the plants, that the Estratos de las Cabras are equivalent to the Narrabeen stage (lower Triassic), the Potrerillos to the Hawkesbury (middle Triassic), and the Cacheuta to the Wianamatta (upper Triassic) of Australia. The Cacheuta flora, however, according to Groeber (*ibid.*, p. 46), does not provide conclusive evidence as to what portion of the Triassic is represented by the Cacheuta series. A comparison of the floral lists for the Triassic of Australia (David, 1950, pp. 432–434) with those for the Cacheuta and equivalent beds (Groeber, 1952) supports this opinion.

According to Groeber (*ibid.*, p. 47) a comparison of the Potrerillos-Cacheuta section with the partly continental, partly marine Triassic section near Los Vilos, Chile, indicates that most of the Cacheuta series is actually Norian in age. At Los Vilos there is a *Dicroidium* flora, which is also found in the Cacheuta series. Comparison of the eruptives from the Los Vilos section and the Potrerillos-Cacheuta beds indicates great similarity in composition. In the marine strata at Los Vilos there is a Norian bivalve and ammonite fauna. Weeks (1947, p. 1209) has suggested that the continental Triassic of northern Mendoza and adjacent areas represents an eastward equivalent of the upper Triassic marine sediments in Chile. The Estratos de Las Cabras, Estratos de Potrerillos, and Estratos de Cacheuta are therefore regarded as Norian, and the Estratos de Rio Blanco only are considered to be Rhaetic.

Kummel and Fuchs (1953) have placed both the *Halobia* beds of the Los Vilos region in Chile and the lower part of the Cacheuta series (Potrerillos and Cacheuta) in the Karnian. The Victor beds (Rio Blanco?) are regarded by them as Norian. It is probable, however, that the red conglomerate and variegated shales at the top of their section are part of the Divisadero Largo, which is Deseadan (lower Oligocene) in age (Simpson and Minoprio, 1949).

The age of *Mendocinia,* which is entirely restricted to the Estratos de Potrerillos of the Cacheuta series, is therefore Norian on the basis of present evidence. The youngest previously known perleidid (*Perleidus altolepis*) occurs in the Perledo beds of the Alpine region, which are placed at the top of the middle Triassic, or possibly at the base of the upper Triassic.

TAXONOMY AND DIAGNOSIS

FAMILY PERLEIDIDAE

GENUS *MENDOCINIA* BORDAS, 1944

Mendocinia BORDAS, 1944, Physis, vol. 19, no. 54, p. 458.

GENOTYPE: *Mendocinia brevis* Bordas.

GENERIC DIAGNOSIS: Fusiform, moderately deep-bodied fishes attaining a length of about 60 mm., and differing from other members of the family Perleididae in the following combination of characters: Skull short anteroposteriorly and relatively deep, nearly one-fifth of total body length. External skull bones thin and without ornamentation. Rostrum sloping, rather than blunt as in *Perleidus* and *Meridensia*. Postrostral bone wide ventrally, narrow where it meets the frontals. Nasal bones forming anterior border of orbit, wider dorsally than ventrally. Paired rostrals and dentigerous premaxillaries apparently present. Frontals about twice the length of the rectangular parietals. Dermopterotic narrow and elongated. Suprascapulars separated. Maxillary very narrow anteriorly, expanded posteriorly, with a rounded posterior border. Suspensorium vertical. Wedge-shaped suborbital (or supraspiracular) and dermohyal (or antopercular) present. Preopercular with infraorbital process. Opercular slightly smaller than subopercular. Branchiostegals present. Mandible tapering towards symphysis. Marginal teeth on premaxillary, maxillary, and dentary conical and pointed. Teeth on prearticular stout and blunt as in *Perleidus madagascariensis*. Supracleithrum and cleithrum typical for family and without ornamentation. Postcleithra apparently absent.

All fins lacking fringing fulcra, but with a few basal fulcra. Pectoral fin large, with 12 rays. Pelvic fin smaller than pectoral, origin near middle of trunk, with about seven rays. Dorsal fin remote, origin about midway between origins of pelvic and anal fins, consisting of about 14 rays. Anal fin with 12 rays, origin behind that of dorsal. Rays of unpaired fins equal in number to endoskeletal supports. Caudal fin hemiheterocercal, moderately cleft, equilobate, composed of about 20 rays.

Scales thin, smooth, with straight posterior border. Anterior flank scales three times as deep as broad, decreasing in depth in other parts of body.

Mendocinia brevis Bordas, 1944

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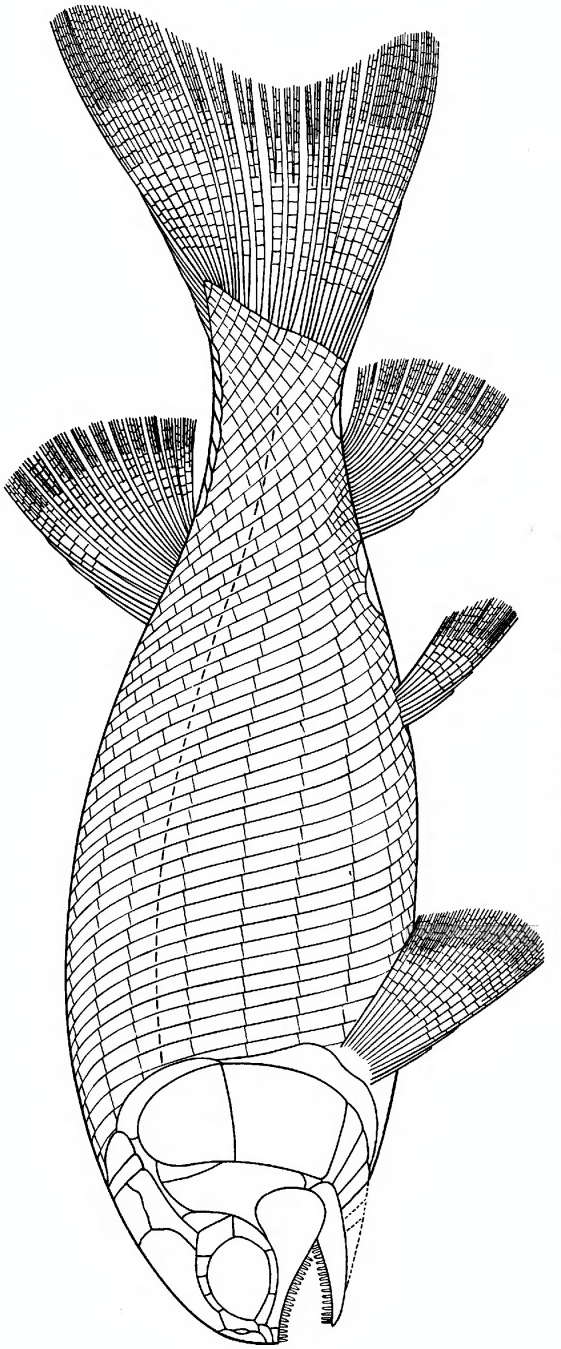

FIG. 1. *Mendocinia brevis*. Reconstruction. × 4.

No. 15.351; two nearly complete specimens figured by Bordas (1944, pl. 2).

SPECIFIC DIAGNOSIS: Same as for genus.

Chiotti, in his unpublished thesis (MS), has recognized a second species of *Mendocinia* called *M. grandis*. This species is also mentioned by

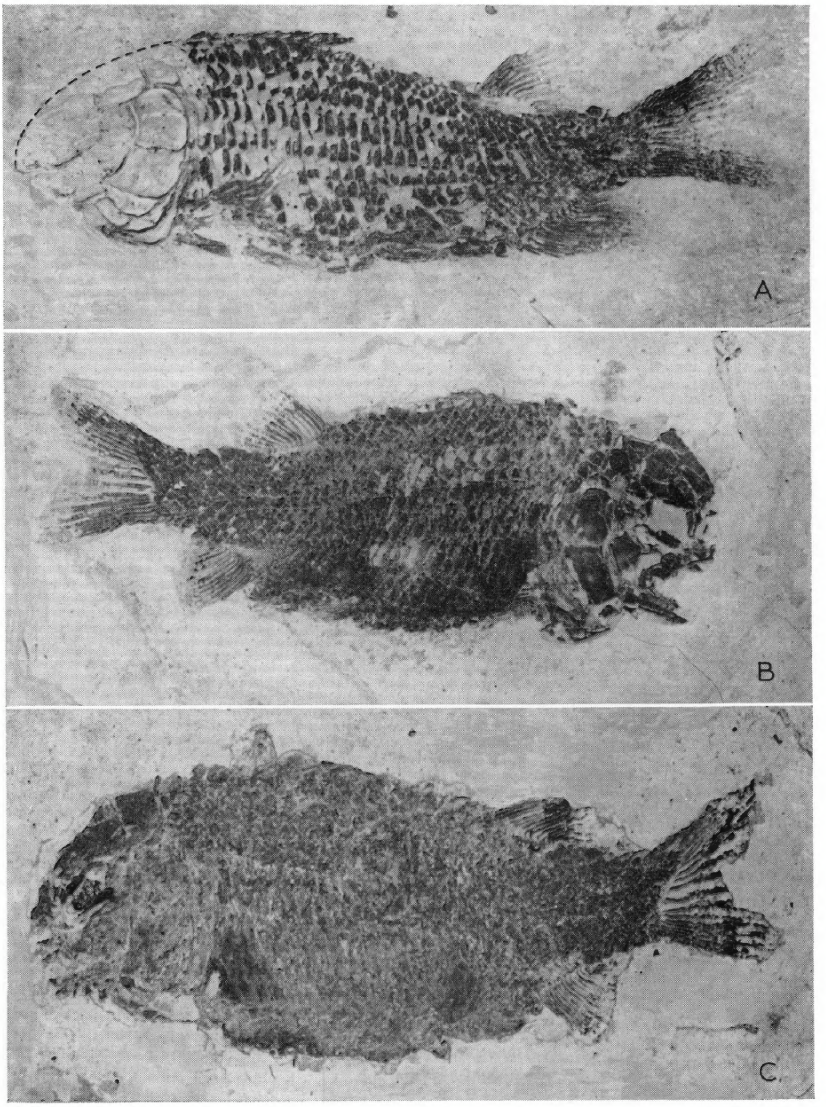

FIG. 2. *Mendocinia brevis*. A. A.M.N.H. No. 8278. B. A.M.N.H. No. 8282. C. A.M.N.H. No. 8279. All × 2.

Groeber (1952, p. 48), without diagnosis or illustration, and is attributed to Bordas. The latter, however, does not mention *grandis* in his only published paper on *Mendocinia.*

Apparently *M. grandis* (*nomen nudum?*) is distinguished from *M. brevis* on the basis of relative body depth. The former is supposed to have a shallower, more fusiform outline. In the sample available for this study, three individuals have a smaller maximum depth in proportion to their length than the others (fig. 2). The deeper-bodied and more shallow-bodied individuals frequently occur together on the same bedding plane, and were obviously buried at the same time. Since several species of various living actinopterygian genera may inhabit the same small body of water, the problem of whether or not two species of *Mendocinia* are, in fact, represented here must be considered. Although two species preserved in this manner could differ in their ecological requirements in life, such differences would not necessarily be evident following preservation.

The fin ray and scale row counts, as well as the details of the dermal skull pattern, are apparently the same in both types. In an effort to resolve the species problem, seven different measurements were made on complete specimens ranging from 19.5 mm. to 48 mm. in standard length. These measurements are evaluated in a series of regressions (fig. 3), with the figures for standard length plotted on the horizontal axis, and the other measurements on the vertical axis. In general, the regressions show a high degree of correlation, suggesting that the sample is homogeneous. In the regression (D) for standard body length and maximum body depth, however, the points for the three shallow-bodied individuals are well separated from the others, and appear to fall on a line with a different slope (the black triangles superimposed on regression E). Several explanations may be offered for this situation which reduce the probability of the presence of a second species, based on the dubious criterion of a slight difference in body depth. First, the available sample may be too small to indicate the actual range of variation in this population. Secondly, several populations (local races) of a single species may be represented in the sample, with minor differences in the mean body depth. Lastly, body depth may be an expression of sexual dimorphism. In regard to the accuracy of the body depth measurements, the high correlation in regression D indicates that it is possible to make such measurements in spite of the compression of the body following preservation.

Horizon and Locality: *Mendocinia* is known to occur only in the Estratos de Potrerillos of the Cacheuta series at a locality near the town of Challao, which is a few kilometers west of the city of Mendoza, Prov-

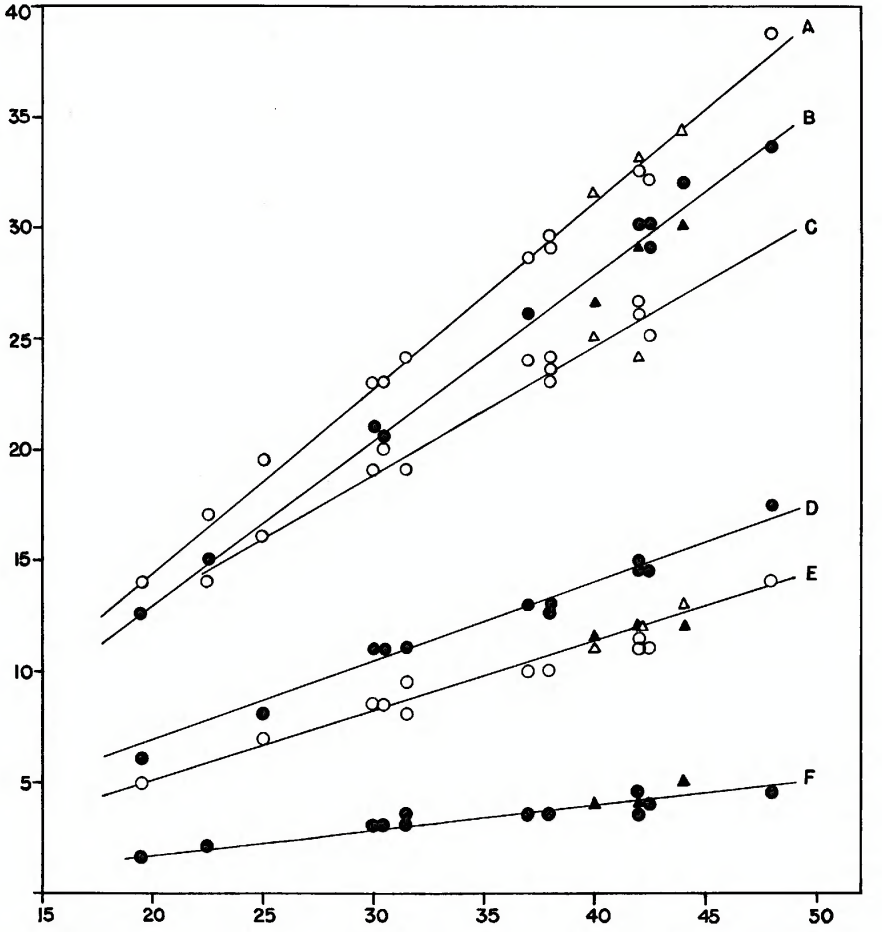

FIG. 3. *Mendocinia brevis*. Graph, in millimeters, of body length minus caudal fin (horizontal axis), and of distances from (A) tip of snout to origin of anal fin, (B) tip of snout to origin of dorsal fin, (C) tip of snout to origin of pelvic fin, (D) maximum body depth, (E) tip of snout to posterior border of opercular, (F) maximum width of opercular.

ince of Mendoza, Argentina. Specimens representing a considerable size range occur together in a finely laminated shale, in association with indeterminable plant fragments, at a horizon near the middle of the Estratos de Potrerillos.

REFERRED SPECIMENS: A.M.N.H. Nos. 8276–8295, including numerous complete specimens, as well as partial skulls and portions of the body. Even the smallest specimens are entire, and there is no evidence of dissociation prior to burial.

DESCRIPTION

BODY FORM: The compact body form of *Mendocinia* closely resembles that of *Manlietta* (Wade, 1935, pl. 9, fig. 1) among the perleidids (fig. 1). The maximum depth, about midway between the posterior border of the skull and the pelvic fins, is somewhat less than one-quarter of the total body length. The skull enters into the total length about four and one-half times. The dorsal and anal fins are remotely situated as in *Manlietta* and *Pristisomus*.

It is rarely possible to make a complete restoration of a fossil fish from a single specimen. The usual composite drawing, if carefully executed, represents all the available information on the skull pattern, body form, fins, and squamation. The shape and depth of the body, particularly in the trunk area, are obviously related to the shape and width of the cross section in that area. In most restorations, some allowance is made for deepening of the body through compression, but frequently the resulting body outline is deeper than the fish was in life.

The problem of maximum body depth can be solved, in part, by an analysis of the squamation pattern in the manner described by Breder (1947). The scale rows of an actinopterygian or choanate fish are arranged according to definite mathematical lines. A single diagonal scale row, particularly in a form with heavy scales like *Lepisosteus* (*ibid.*, fig. 30B), can be observed to wind around the body in a continous band from the head to the tail. An intersecting row of scales, somewhat less clearly defined, wraps around the body in the opposite direction. The angles of intersection of these rows (*ibid.*, p. 394, table 6), as well as the number of complete revolutions of the rows, are clearly related to the body form of the living fish. The angle should be measured in the deepest part of the body where the scale pattern is not interrupted or altered by fin insertions. Breder (*ibid.*, p. 394, table 6) has tabulated this angle, together with the depth-length ratio of the body, for a number of living and fossil actinopterygians and choanates. The graphic treatment of these data (*ibid.*, p. 395, fig. 35) demonstrates that, in general, an increase in the depth of the body is correlated with a decrease in the angle of the intersecting scale rows.

In *Mendocinia brevis* the angle of intersection is about 33 degrees and the length-depth ratio is 34. According to table 6 in Breder's paper, these determinations agree with the figures for the cichlid *Tilapia macrocephala*. The restored body outline of *Mendocinia* corresponds closely with that of *T. macrocephala*, as may be demonstrated by superimposing their body outlines.

This sort of analysis does not provide direct evidence on the maximum

width of the body in the region of greatest depth. For certain of the perleidids, some conclusions may be drawn from a cast of a natural external mold of *Perleidus madagascariensis*. The skull roof in this specimen (A.M.N.H. No. 8297) shows no evidence of crushing. When the cheek and opercular area are brought into normal alignment with the roof, the maximum width of the body may be estimated. Although this estimate is admittedly subject to some error, as the greatest body width in some actinopterygians may be well behind the opercular area, there is clear indication, in *Perleidus,* of a fairly rounded cross section. This sort of body form is related to the nearly flat skull roof, a character probably shared also by *Meidiicthys, Meridensia, Colobodus,* and possibly *Pristisomus*. In the genera with a relatively deeper body, such as *Procheirichthys* and *Mendocinia,* it is reasonable to conclude that the body was more compressed. The skull roof in these forms was apparently not so flat as in *Perleidus* and the other genera mentioned above.

Skull: The pattern of the skull roof (figs. 4 and 5) agrees closely with that of the other perleidids. The extrascapulars (tabulars) are rectangular and narrow anteroposteriorly. The parietals are quadrangular and nearly one-half of the length of the frontals as in *Pristisomus* and perhaps *Colobodus*. Behind the orbits, the frontals show a marked transverse expansion which is apparently not characteristic of the other known perleidids, with the possible exception of *Manlietta* (Wade, 1935, fig. 29). As in most other members of the family, the dermopterotic (supratemporal) is narrow and appears to be in direct contact with the dermosphenotic. In *Meidiicthys* and possibly in *Meridensia* (figs. 7 and 8), these elements are separated by a supraspiracular.

The circumorbital series is composed of three small supraorbitals, the dermosphenotic, three infraorbitals, and the nasals. A triangular element, which may be regarded as either a suborbital or supraspiracular, occupies the space between the dermosphenotic and the preopercular.

The postrostral is relatively smaller than in *Perleidus, Meidiicthys, Meridensia,* and *Pristisomus,* suggesting that the snout was not truncated as in these genera but had a more sloping alignment with the frontals. As preserved, the postrostral has a characteristic, flask-shaped outline. The broad, rounded ventral margin of the postrostral is in contact with the narrow paired rostrals, the constricted lateral margins meet the nasals above and below the relatively large, elliptical nares, and the narrow dorsal border has a restricted contact with the frontals and anterior supraorbitals. The nasal is considerably broader dorsally, where it meets the frontal and anterior supraorbital, than it is ventrally where it is in contact with the rostral and anterior infraorbital.

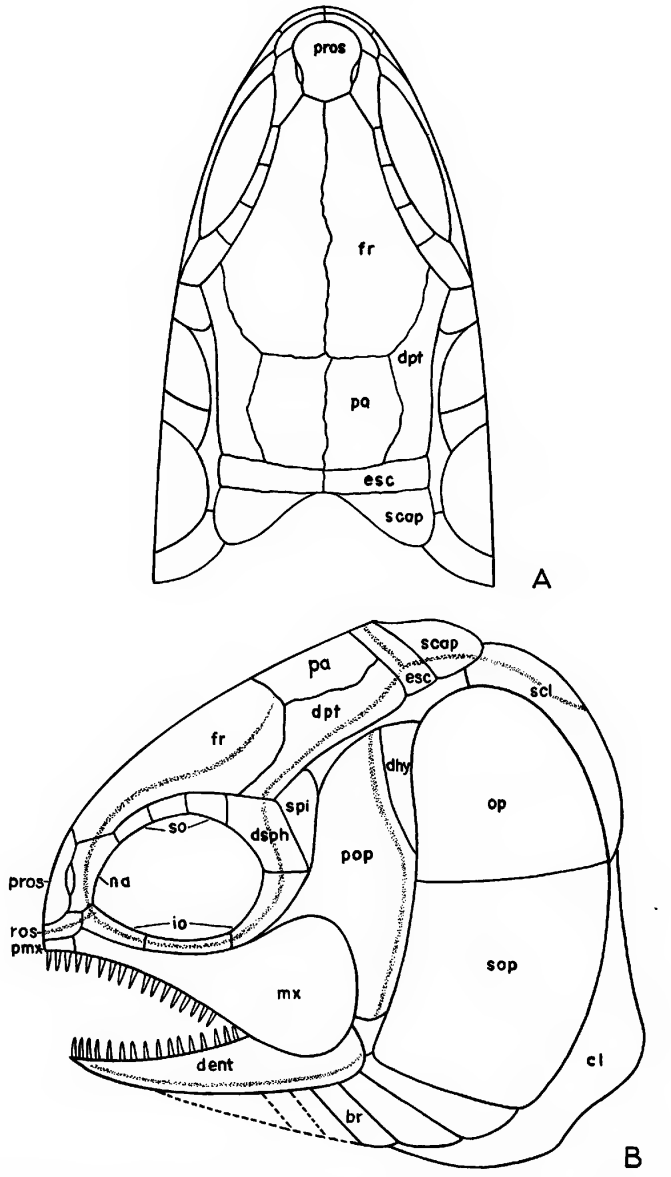

FIG. 4. *Mendocinia brevis*. Reconstruction of skull. A. Dorsal view. B. Lateral view. *Abbreviations*: br, branchiostegal; cl, cleithrum; dent, dentary; dhy, dermohyal (antopercular); dpt, dermopterotic; dsph, dermosphenotic; esc, extrascapular; fr, frontal; io, infraorbital; mx, maxillary; na, nasal; op, opercular; pa, parietal; pmx, premaxillary; pop, preopercular; pros, postrostral; ros, rostral; scap, suprascapular; scl, supracleithrum; so, supraorbital; spi, supraspiracular (suborbital); sop, subopercular.

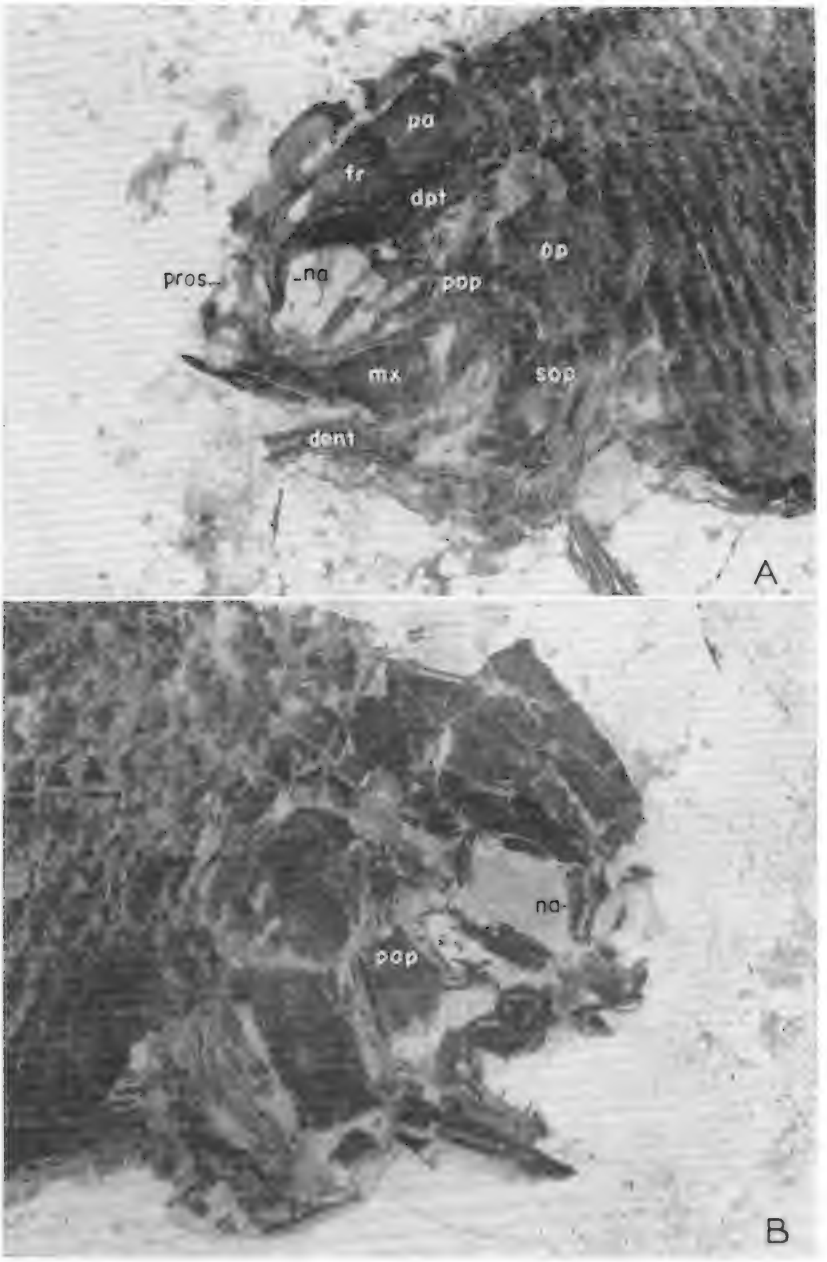

FIG. 5. *Mendocinia brevis*. Skull in lateral view. A. A.M.N.H. No. 8296. B. A.M.N.H. No. 8282. Both × 5.

Paired, dentigerous premaxillaries are apparently present, situated below the rostrals as in *Perleidus,* rather than anterior to them as in *Meidiicthys.*

The postorbital expansion of the perleidid maxillary is either lobe-shaped, with a rounded posterior margin, or essentially triangular, with a nearly straight posterior border which slopes anteroposteriorly. *Meridensia, Pristisomus,* and *Mendocinia* fit into the first category, while *Meidiicthys, Perleidus, Dollopterus, Colobodus,* and the other Australian genera (excluding *Pristisomus*) belong, in general, to the second category (see figs. 7 and 8). The preopercular of *Mendocinia* is similar to that of *Pristisomus* in being markedly constricted between the maxillary and the subopercular. In the other genera, the preopercular is wedge-shaped in this area. The acuminate infraorbital process of the preopercular is apparently better developed in *Mendocinia* than in the other perleidids, although this character may be quite variable within a genus. The process is absent in *Perleidus madagascariensis,* but present in *P. woodwardi* (Stensiö, 1921, fig. 81).

A dermohyal (or antopercular) is situated between the opercular and the preopercular as in *Perleidus, Meidiicthys,* and probably *Pristisomus.* The opercular is slightly smaller than the subopercular. The relative size of these elements is variable within the family and has little taxonomic significance. Branchiostegals are present, but the total number cannot be determined.

The mandible (fig. 6) is similar to that of the other well-known genera in form and proportion. In addition to the conical, pointed, marginal teeth present on the premaxillary, maxillary, and dentary, there is evidence, in one specimen (A.M.N.H. No. 8287), of a row of broader,

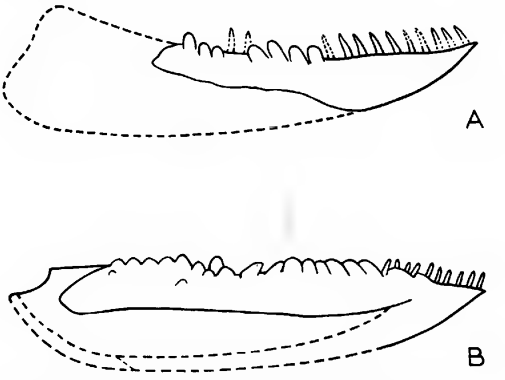

FIG. 6. Dentary in median view. A. *Mendocinia brevis.* A.M.N.H. No. 8287. × 10.5. B. *Perleidus madagascariensis* (after Lehman, 1952).

rounder teeth on the prearticular. Similar teeth are present on the prearticular and ectopterygoid of *Perleidus madagascariensis* (Lehman, 1952, fig. 89B), and are also known to occur in *Meridensia* (Brough, 1939) and *Colobodus* (Stolley, 1920, pl. 11, figs. 2a, 3).

The arrangement of the sensory canals is typical and requires no special comment. A rostral or ethmoidal commissure is indicated by the well-developed canal which traverses the entire width of the rostral bones.

PAIRED FINS: The suprascapulars of *Mendocinia* do not meet, and available evidence indicates that they are usually separated in the other perleidids. The other bones of the dermal pectoral girdle show no unusual features. Postcleithra are apparently absent. The large pectoral fin is composed of about 12 rays which are segmented for about one-half of their length. The smaller pelvic fin is situated nearer to the anal than to the pectoral. It has about seven distally segmented rays.

UNPAIRED FINS: The dorsal and anal fins apparently have a more remote position than in the other known perleidids, with the exception of *Manlietta* (Wade, 1935, pl. 9, fig. 1). The dorsal fin consists of about 14 rays, and the anal, which is slightly smaller than the dorsal, of 12 rays. Both fins are segmented distally. The endoskeletal supports of the unpaired fins are visible in several specimens, and they agree in number with the lepidotrichia.

The caudal fin is equilobate and has the reduced heterocercal condition generally characteristic of the perleidids. It has 22 bifurcated and segmented rays which are closely grouped towards the dorsal and ventral borders of the fin. In the center of the fin, the rays are always separated as in *Manlietta* and *Pristisomus*. The caudal fin is relatively large for a perleidid, nearly one-fifth of the entire body length.

Fringing fulcra are not present on any of the fins, and the basal fulcra are few and slender. In other perleidids, the fulcra are variously developed. Both fringing and basal fulcra are present in *Meidiicthys, Perleidus,* and *Colobodus*. Brough (1939) was able to find only the basal type in *Meridensia,* and even these are absent on the caudal fin.

SQUAMATION: Although the scales are generally thin and poorly preserved, it has been possible to work out the scale pattern in some detail. There are about 40 vertical scale rows along the lateral line between the posterior border of the supracleithrum and the base of the caudal fin. The scales are about three times as deep as wide on the anterior flank area. They decrease in depth dorsally, ventrally, and caudally. The surfaces of the scales are smooth, and the posterior margins show no evidence of pectination. In thin section, there is no clear indication of the cosmine

layer, although it may be present. It is developed only in the posterior halves of the scales in *Perleidus* (Stensiö, 1932, fig. 70).

Bordas (1944, p. 458) is of the opinion that *Mendocinia* has an anterior dorsal fin. In some specimens there is evidence of enlarged ridge scales in front of the dorsal (fig. 2A) which might be confused with the base of a fin. Ridge scales are also present on the dorsal and ventral borders of the peduncle and in front of the anal fin.

DISCUSSION

Brough (1931, 1936) has pointed out that the Perleididae, like the other families included in the Subholostei, possess a combination of retained palaeoniscoid characters and definitive holostean characters. In some families, such as the Catopteridae, the included genera show a considerable range in structural pattern for certain character complexes. The known perleidids, on the other hand, have a relatively stable pattern.

With the possible exception of the reduction in the caudal body lobe, the functional significance of the modifications involved in the palaeoniscoid-holostean transition is poorly understood. At least some of the changes in the skull are interrelated, but these changes frequently occurred independently of modifications in the fins or scales. The different subholostean families show various possible combinations of palaeoniscoid and holostean characters, but in only one known family, the Parasemionotidae (placed in the Holostei by Lehman, 1952), are the modifications combined to produce a possible holostean ancestral group.

The monophyletic versus the polyphyletic origin of the holosteans has been discussed recently by Rayner (1941, 1948), Westoll (1944), and Schaeffer and Dunkle (1950). This problem is not considered again here, because the perleidids offer little towards its elucidation.

The perleidid neurocranium is known only for the genus *Perleidus* (Stensiö, 1932; Lehman, 1952, 1953). It is essentially palaeoniscoid in character and shows none of the subdivisions present in the holostean neurocranium. Rayner (1948, p. 335) has pointed out that the neurocranium and the skull roof are among the most stable parts of the actinopterygian skull. The skull-roof pattern of the perleidids is neither more nor less palaeoniscoid, or holostean, than that of any other subholostean group. The parietal area shows less tendency towards subdivision (or multiplication?) of dermal elements than that of the catopterids or pholidopleurids, but in large samples of *Perleidus piveteaui* and *P. madagascariensis* individuals occur with an apparently random increase in the number of parietals over the usual two (Lehman, 1952, p. 140).

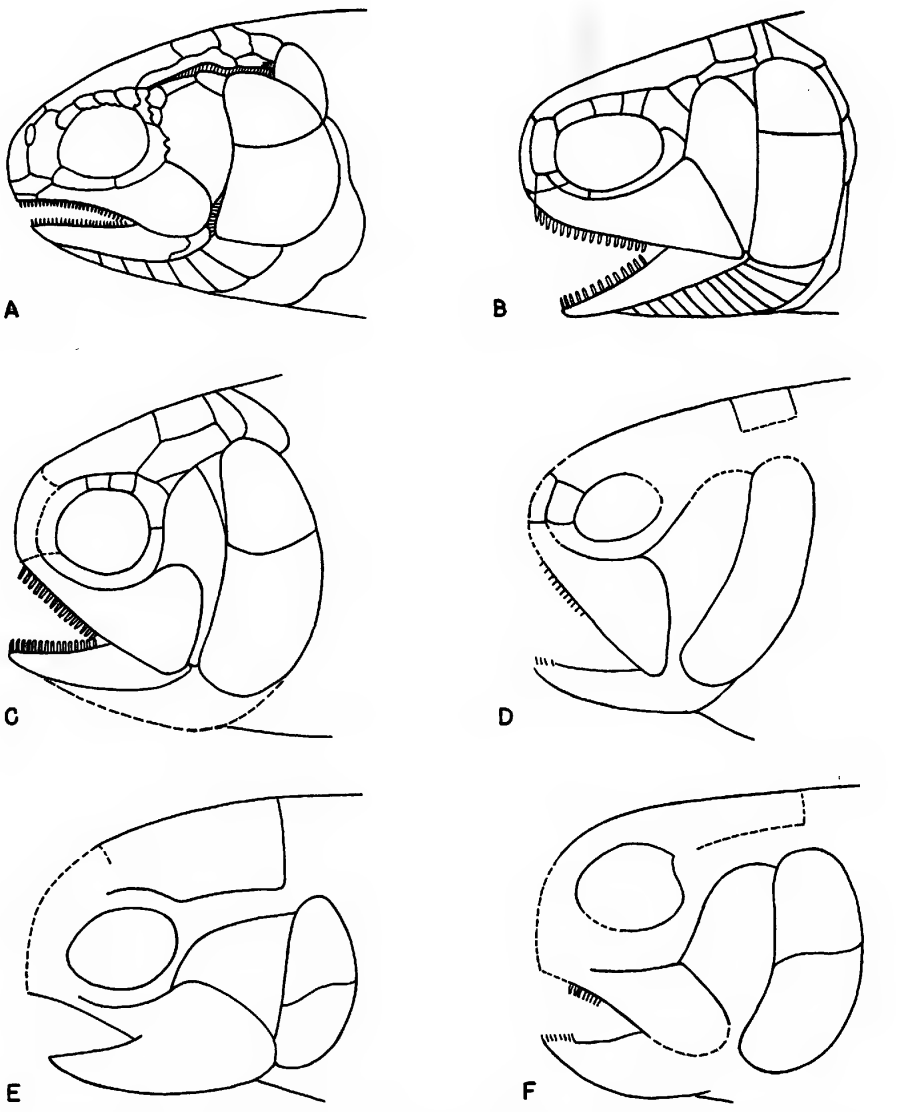

FIG. 7. Series of perleidid skulls in lateral view. A. *Perleidus madagascariensis* (after Lehman, 1952, and specimens). B. *Meidiicthys browni* (after Brough, 1931). C. *Pristisomus gracilis* (A.M.N.H. No. 8275). D. *Tripelta dubia* (after Wade, 1939). E. *Chrotichthys gregarius* (after Wade, 1939). F. *Zeuchthiscus australis* (after Wade, 1939).

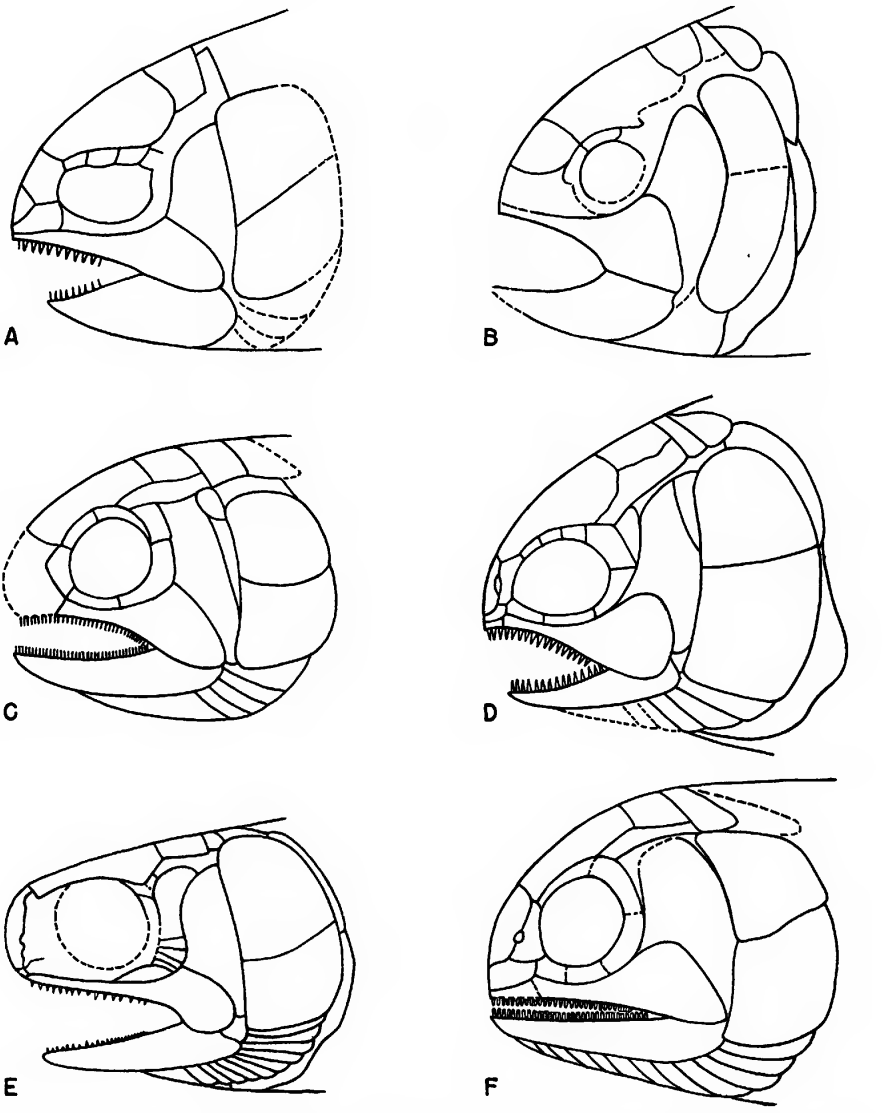

FIG. 8. Series of perleidid skulls in lateral view. A. *Manlietta crassa* (after Wade, 1935). B. *Procheirichthys ferox* (after Wade, 1935). C. *Dollopterus brunsuicensis* (composite, after Stolley, 1920). D. *Mendocinia brevis*. E. *Meridensia meridensis* (after Brough, 1939). *F. Colobodus maximus* (composite, after Stolley, 1920, and Stensiö, 1921).

In all the known perleidid genera but two, the snout is typically palaeoniscoid, with the nasals separated by a large postrostral. In *Manlietta* and *Procheirichthys* (Wade, 1935), however, the nasals meet in the midline, and the postrostral is absent. This situation apparently occurs only in the parasemionotids among the other subholosteans. If it is assumed that these genera are correctly allocated to the Perleididae, there is here evidence that the parasemionotid type of snout pattern developed more than once in the subholosteans and within a family where all the other genera have the old palaeoniscoid snout arrangement.

The variation in cheek pattern in the perleidids, discussed above, is suggestive of that found in the haplolepids. As Westoll (1944, p. 91) points out, the triangular preopercular and the maxillary expansion of *Haplolepis corrugata* resemble the condition in perleidids such as *Meidiicthys*. The form of the preopercular and maxillary in *Pyritocephalus sculptus* is somewhat similar to that of *Pristisomus* and *Mendocinia*. Westoll's comment that the pattern itself has little or no functional significance but is correlated with the shift in the angle of the suspensorium and related changes in the jaw mechanism is surely correct. The cheek pattern of the perleidids is essentially palaeoniscoid. There is no observable trend towards elimination of the maxillary-preopercular articulation or towards the development of an interopercular.

The reduction in the segmentation of the paired fins, the equaling of the fin rays and radials, and the reduction of the body lobe in the tail are all advanced characters. The reduction or apparent absence of fulcra in some genera (*Meridensia, Mendocinia, Manlietta*) may have some functional meaning, but cannot be regarded as an advanced condition, as most holosteans have well-developed fringing and basal fulcra.

The scale structure of the perleidids is poorly known. Whether or not the reduction in the cosmine layer noted in *Perleidus* (Stensiö, 1932) is characteristic of the group remains to be determined.

The family Perleididae was erected by Brough (1931) to include *Perleidus, Colobodus, Dollopterus, Meridensia, Meidiicthys, Cleithrolepis,* and *Hydropessum.* These genera were considered to differ from the catopterids, with which they had formerly been included, by the more advanced fin structure and by certain other differences in the skull and fins. In 1932 Stensiö partly revised the diagnosis of the Perleididae, adding endocranial characters (from *Perleidus*). The diagnosis was still further altered by Wade (1935) with the exclusion of *Cleithrolepis* and *Hydropessum.* Berg (1940) erected the Order Perleidiformes to include the Perleididae and two other families (Teleopterinidae and Cleithrolepidae) which he believed to share certain perleidid characters. *Teleop-*

terina, the only genus in his family Teleopterinidae, is a haplolepid probably identical with *Pyritocephalus* (Westoll, 1944). The Cleithrolepidae possess some retained palaeoniscoid characters in common with the Perleididae, but, as Wade (1935) has demonstrated, there is no reason to believe that these families are closely related. Although Berg made the laudable attempt to erect a vertical category, available evidence does not support the inclusion of these families in a separate order. In a recent study of *Perleidus,* Lehman (1952, p. 145) has further considered the differences between the perleidids and the catopterids. He is of the opinion that the two families can be separated only by the presence, in the perleidids, of a triturating dentition (known in only a few genera) and by the reduced number of lepidotrichia in the unpaired fins.

This brief history of perleidid systematics emphasizes the difficulty of preparing a reasonably restrictive family diagnosis. In the definition of a group such as the Perleididae, which lacks obviously adaptive characters fitting it for a particular, though somewhat broader niche than that occupied by any of the included genera, the diagnosis must include a combination of those primitive and advanced characters that most clearly distinguish it from all other subholostean families. The main difficulty in the defining of a family of fossil fishes (and most other types of fossils) is that knowledge of the included genera is not uniform, and by the nature of the preservation probably never can be. The diagnosis, therefore, is frequently based partly on fact, partly on the probability that characters observed in one or a few genera occur in all the genera of the family. Certain characters that have frequently appeared in the diagnosis of the Perleididae (in the braincase and scale structure) are actually known to occur only in *Perleidus.* Structural complexes, such as the neurocranium, which are known in only a few genera among the subholosteans and therefore can be considered in only a general way, are of little value in diagnosis. The fact that the perleidid neurocranium is of the palaeoniscoid type, in common with the few other described subholostean neurocrania, is of interest in connection with the evolution of the group, but it does not aid in providing a restrictive diagnosis.

In the light of present knowledge, the Perleididae may be diagnosed as follows: Body elegantly to deeply fusiform. Snout with nasals separated by postrostral bone, or nasals meeting and postrostral absent. Paired premaxillaries and rostral present. Maxillary with concave dorsal border, expanded posteriorly, and attached to preopercular. Nasals forming anterior margin of orbit; antorbital absent. Preopercular wedge-shaped, or constricted behind maxillary. Suspensorium moderately oblique to vertical. Suborbital, "supraspiracular," and dermohyal (antopercular)

bones may be present or absent. Opercular and subopercular subequal. Interopercular absent. Branchiostegals present. Mandible without coronoid process. Low, rounded teeth on pterygoids (*Perleidus, ?Colobodus*) and on prearticular (*Perleidus, Mendocinia, Colobodus*). Basal and fringing fulcra on fins variously developed, possibly absent in a few genera. Fin rays segmented in distal portion only, except in caudal where rays of some genera are completely segmented. Rays of dorsal and anal equal in number to radials. Caudal fin scarcely to moderately forked, hemiheterocercal. Scales and dermal bones smooth, or with ornamentation. Scale structure approaching lepidosteoid type, cosmine layer reduced (*Perleidus*).

On the basis of this diagnosis, the Catopteridae may be distinguished by the excess of rays over radials in the dorsal and anal fins, and by the presence of only one, modified branchiostegal. The Platysigidae are distinctive in having an incipient interoperculum and a broad coronoid process on the mandible. The Cephaloxenidae show differences in skull pattern, squamation, massiveness of skull bones, and fin structure. The Peltopleuridae also have a different scale pattern and skull pattern, as well as a weak dentition. In the Luganoiidae the jaws are small, the maxillary is separated from the preopercular, the skull roof is greatly constricted between the orbits, the preopercular is extremely wide ventrally, and the flank scales are very deep. Although the Aetheodontidae share a crushing dentition with at least some of the perleidids (as does *Cephaloxenus*), Brough (1939) considers the family to be distinct. Except for the presence of uniformly small scales and reduced parietals, there seem to be close resemblances to the perleidids.

The Ptycholepidae are obviously distinctive from the perleidids in skull pattern and scale form. The Parasemionotidae, in possessing an interoperculum and a free maxillary, are clearly advanced over the perleidids. The resemblance in snout structure between certain presumed perleidid genera and the parasemionotids is discussed above. In the Pholidopleuridae the parietals are greatly subdivided, and the rays of the dorsal and anal fins exceed the number of the basal supports. The Saurichthyidae, Cleithrolepidae, and Bobasatraniidae are specialized in such a way that they cannot be confused with the perleidids.

From this brief and incomplete comparison of the subholostean families (as listed in Romer, 1945) it is evident that the particular combination of characters present in the Perleididae is not duplicated in a significant way by the character complexes of the other families. The distinction between the perleidids and catopterids cannot now be based on all the differences listed by Brough (1931), but the two main char-

acters that do permit separation of these families are consistent and taxonomically important.

According to the above diagnosis of the Perleididae, *Mendocinia* is a typical member of the family. The morphology of this genus supports the conclusion that the perleidids had a rather fixed structural plan which shows advance towards the holostean level in the paired fins, the reduced body lobe in the tail, and the reduction in the cosmine layer of the scales. The enlarged pectoral fins of *Dollopterus* represent perhaps the most striking specialization within the family.

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